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LETTER

REPLY TO SNOWDON ET AL. AND PIEPHO:

Genetic response diversity to provide yield stability of cultivar groups deserves attention

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Climate resilience refers to the capacity of a system to buffer core functions against climate-related uncertainty and variability (1). The occurrence of diversity in responses to weather variability within a functional group or species (2, 3), such as European wheat that supplies bread and pasta, can ensure a reasonable yield regardless of weather conditions and provides genetic material for selection under changing climate (4). Genetic diversity is not directly related to response diversity, as shown for forage crops (5). Since most of the forage crop species were distributed among several weather response clusters and most of the clusters contained several species, the genetic closeness did not fully explain responses to critical weather conditions. This phenomenon may represent a keystone for breeding and thus deserves to be explored further. Indeed, genetic response diversity deserves more attention with respect to yield and quality (6).

The suitability of response diversity to describe agronomic fitness in wheat monocultures is questioned by Snowdon et al. (7), but no arguments are presented. We (8) consider the approach suitable to assess and enhance the resilience of monocultures and thereby increase the stability of total yield under weather variability regardless of whether the complementary cultivars are cultivated on one farm or within a region, national borders, or Europe. Cultivar (or crop) mixtures common in forage cultivation and sometimes used with cereals to enhance resistance to pests have the potential to compensate for losses during the growing season and deserve further study.

Yield potential is not analyzed in our study. We focus on yield stability of a group of cultivars. The potential yield stability under environmental variation is higher if the genetic potential of a group of cultivars with different responses to the environment rather than of a single cultivar is utilized. If cultivars are selected based on empirical data on responses to weather events critical to yield, response diversity has the potential to secure yields and financial returns to farmers through reducing yield variation. In the box within figure 2 of ref. 8, we demonstrate the significance of response diversity to a decline in yield variation, but not to average yield over 7 y. Data from three cultivars with the greatest numbers of observations within one trial location were used, each cultivar representing a different weather response cluster. The statement that there is "no inherent trade-off between yield potential and diversity in weather responses" (8) highlights the opportunity to select a group of cultivars with both response diversity and a high yield potential of each cultivar.

The clustered Europe-wide variety trial data from the 25-y period and the independent country-specific cultivar area data were used to calculate Shannon diversity index values for the weather response clusters on farms. The aim was to assess how many clusters were cultivated and how equally the cultivated hectares were distributed among the clusters. In the response diversity analysis, the weather response clusters were used as diversity units, not accounting for cluster

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variances. Instead, cluster variances were used to demonstrate the relation between resilience and response diversity in figure 2 of ref. 8. We show that while adding clusters one by one, the yield variance of the new cluster combinations declined. Ward's method, which minimizes the within-cluster variances, was used to determine the order in which the clusters were added.

Our findings on the decline of response diversity are questioned by Snowdon et al. (7) based on the results of a metaanalysis (9). However, the metaanalysis reported genetic diversity and not response diversity, did not focus on Europe, and was based largely on data until 2000 (one study, from the United Kingdom, had data to 2005). Thus, the metaanalysis did not cover the period of declining response diversity since 2002–2009 in our study. We found that among the eight studied countries, five showed declines of response diversity on farmers' fields, and two showed plateaued response diversity. An increase was observed only in Finland, with a negligible cultivation area. While wheat yields may still increase in variety trials, the stagnation of farmers' yields in many countries and the increase in interannual variability coincide with our findings.

Some comments of Piepho (10) and Snowdon et al. (7) appear to be based on a misunderstanding of the analytical procedures (Fig. 1). We did not analyze changes in weather variability or yields; nevertheless, such changes would not have confounded our analysis because the structure in the cultivar yield responses to weather events was investigated regardless of the time span, with all 101,000 observations simultaneously included. Snowdon et al. consider that our data imply bias toward small countries with narrow agroclimatic gradients. Our study covered nine European countries, both large and small, including Germany, France, Spain, and Italy, and the agroclimatic gradient spanned from Finland to Italy and from Belgium to Czechia. The broad variation in "ecogeographical forms and species of wheat" (7) as well as in agroclimatic events across the countries in the same analysis ensured the detection of response diversity, if any.

All random effects known to be important were included in our mixed model. Unlike traditionally regarding variety trials, the effect of the classified agroclimatic variables, which presumably correlated strongly with environmental effects (e.g., *year* × *site*), was included in the model. Lower-order interactions were tested for a few agroclimatic variables and were found to be close to zero. Thus, the same simplified model was used for every agroclimatic variable. The denominator of a relative difference was the yield of the category closest to zero, which retains the reversibility of the relative difference in principal component analysis.

We can give access to the trial data with no cultivar names, as allowed by the data owners [supplemental information appendix in ref. 8 (for Spain, contact jordi.doltra@irta.cat)], pending consent regarding France and Slovakia. Connecting the cultivation area data to the trial data requires permission from all of the data owners.

We conclude that breeders need tools to approach response diversity and its genetic basis to complement their current toolbox. We initiated a cocreation process with Nordic breeders (11) continued in Denmark this year.

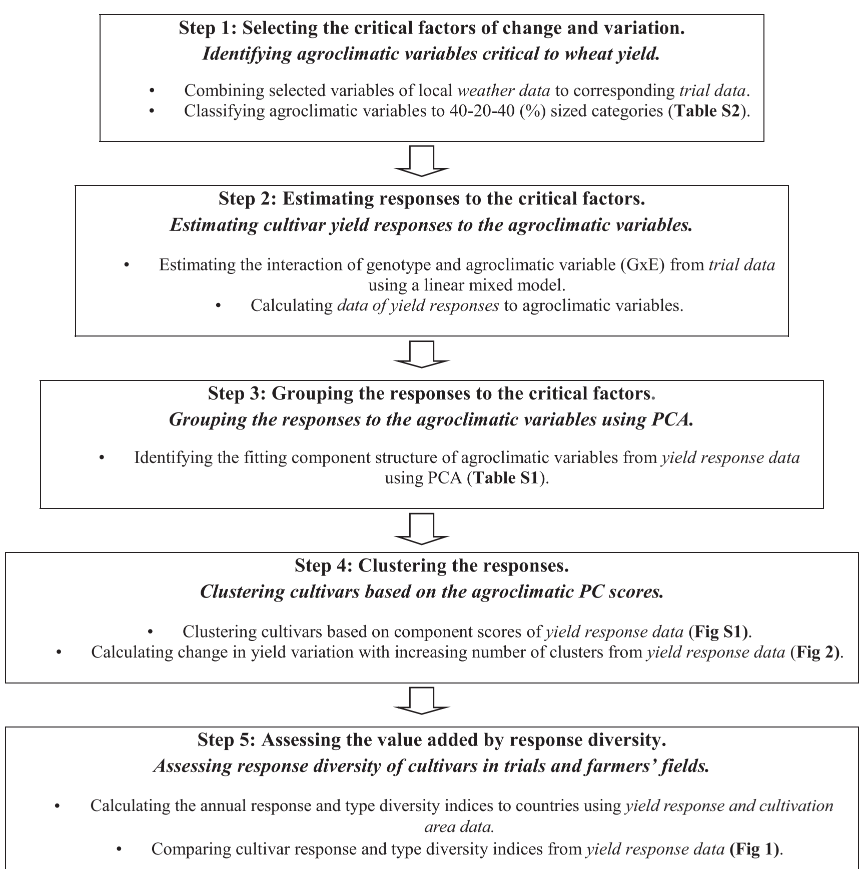

Fig. 1. The proposed response diversity assessment. The steps of the generic procedure are presented in bold type on the first line. The procedure that is applied to the case reported by Kahiluoto et al. (8) is specified for each step in bold type and italics on the second line. Data and analyses related to the figures and tables of ref. 8 are shown in roman font on the lowest lines.

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